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THE VELIGER

A New Species of Leptonacean Bivalve from off Northwestern Peru (Heterodonta: Veneroida: Lasaeidae)

by

JOSEPH ROSEWATER

Department of Invertebrate Zoology, National Museum of Natural History, Washington, D.C. 20560

Abstract. A new species of leptonacean bivalve, *Pseudopythina* ***muris***, has been found in the respiratory cavity of a polychaete, *Aphrodita,* from off northwestern Peru (R/V *Anton Bruun* SEPBOP cruise 16, sta. 625a; cruise 18B, sta. 764). Mature clams are strongly crescent-shaped and are attached by fine byssal threads to elytra of *Aphrodita.* Young stages are moderately equilateral, but show progressive changes in shape until the adult inequilateral condition is achieved. Characteristics of shell and soft part morphology indicate placement of this species in the superfamily Leptonacea, family Lasaeidae. The unusual shape may be an adaptation to life in the respiratory cavity of *Aphrodita.* Examinations of this and other oddly shaped Leptonacea show that some of these anatomical modifications are functional adaptations to the hosts or commensals with which they are associated.

INTRODUCTION

THE R/V *Anton Bruun* carried out nine cruises during the International Indian Ocean Expedition (IIOE, 1963–1964). In 1965, upon returning to the western hemisphere (cruise 10), the *Anton Bruun* began the Southeastern Pacific Biological Oceanographic Program (SEPBOP, 1965–1966), during which eight cruises were undertaken (cruises 11–18, the last consisting of parts A and B). During cruises 16 and 18B, trawls were made in 90–133 m, off northwestern Peru. Invertebrates captured were forwarded to the Smithsonian Institution's Oceanographic Sorting Center, Washington, D.C., where they were sorted and initial identifications were made. Scale worms, Aphroditidae, are normally sent to M. H. Pettibone, National Museum of Natural History, for study. However, since small bivalves were found clinging to ventral surfaces of some specimens, they were sent first to me. The small bivalves were noted externally and, in addition, upon palpation, hard bodies were felt in the normally soft scale worms. The worms were X-rayed revealing the crescent-shaped clams visible in Figure 1A–F. I dissected the scale worms (*Aphrodita japonica* Marenzeller, 1879) revealing a number of the bivalves, ranging from tiny rather normally shaped specimens, as small as 1 mm in length, to larger crescent-shaped individuals, 10.9 mm in length. Comparison with collections and the literature revealed no known species exhibiting the characteristics of the bivalves found in the respiratory cavity of *Aphrodita* (see ROSEWATER, 1983). They are herein described as a new species belonging to the family Lasaeidae.

BOSS (1965) reviewed the commensal relationships of the "Erycinacea" (now Leptonacea; see CHAVAN, 1969, and BOSS, 1982; also see Acknowledgments, herein) and, in an addendum to his paper, mentioned that PONDER (1965) had described the New Zealand leptonacean bivalve *Arthritica hulmei* attached to the elytra of *Aphrodita,* a relationship apparently very similar to the one reported here. Both PETTIBONE (1953) and NARCHI (1969) described the relationship of the east Pacific leptonacean bivalve species *Pseudopythina rugifera* (Carpenter, 1864) with *Aphrodita japonica,* the same worm host involved in the present study. The former was said by Pettibone to occur in the respiratory cavity of the worm, and both Pettibone and Narchi report it to attach externally. It is also known to attach to the crustacean *Upogebia.*

The new species is reminiscent of another crescent-shaped bivalve, *Curvemysella paula* (Adams, 1856), from the Indo-Pacific, although the two differ in details of hinge structure, and in mature stages the new species possesses a more strongly crescent-shaped shell that is equivalve, strongly hypertrophied posteriorly, and narrowed anteriorly. Young stages are moderately equilateral, but show progressive changes in shape until the adult inequilateral condition is assumed (see Figure 2).

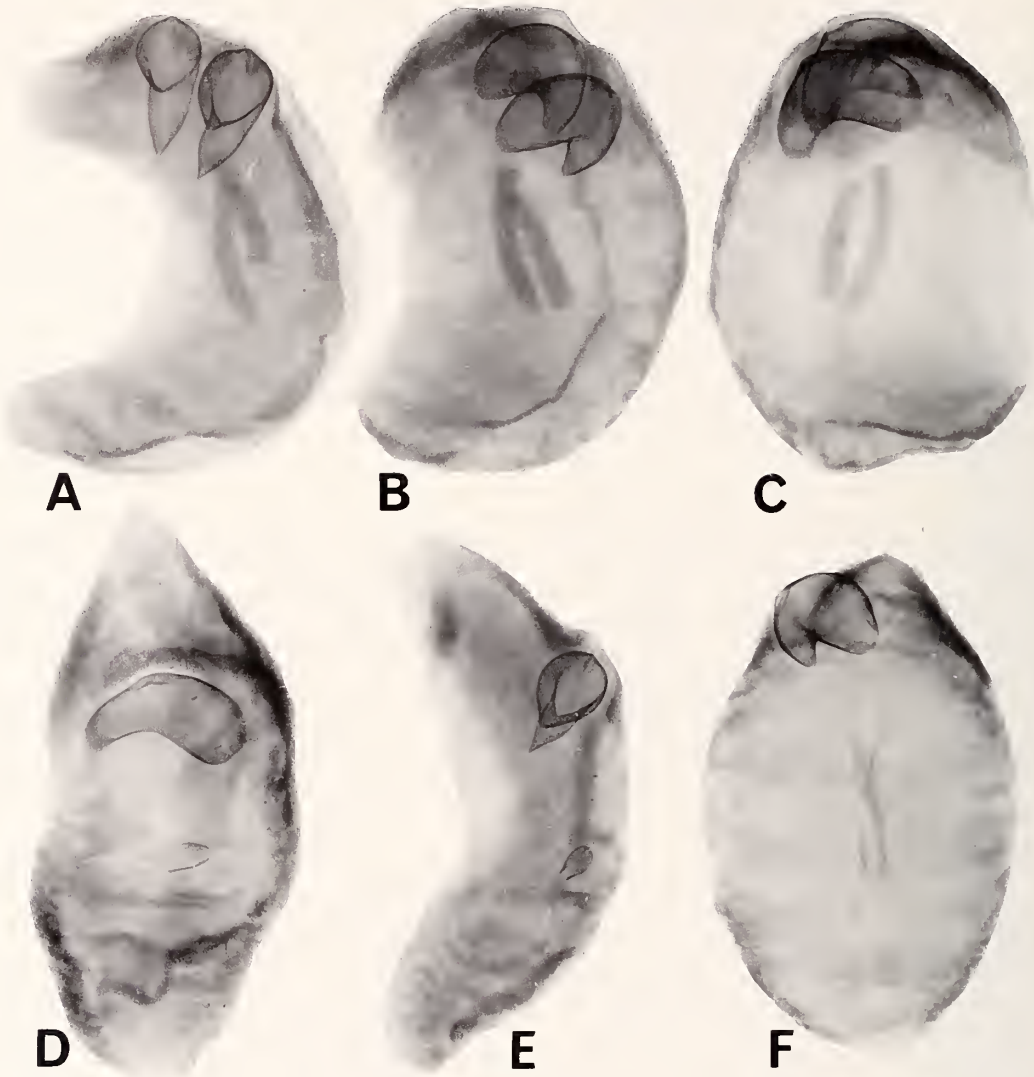

Figure 1

X-rays showing *Pseudopythina* ***muris*** spec. nov. *in situ*, in respiratory cavity of *Aphrodita japonica*; larger clams are nearer the posterior end of worm (worms 4–5 cm in length). A–C. Same individual from different angles. D–E. Different individual. F. Another individual. Note in E and F, tiny clams scattered through worm's respiratory cavity.

TAXONOMY

Family Lasaeidae Gray, 1847

GRAY, J. E. 1847:192 [as Lasiadae].

In a recent review of the phylum Mollusca, BOSS (1982) characterized members of the bivalve family Lasaeidae (Subclass Heterodonta: Order Veneroida: Superfamily Leptonacea) as being equivalve, variously shaped, thin, fragile, compressed to more-or-less inflated, umbos submedian, usually less than 20 mm in length, dimyarian, adductors subequal, pallial line simple, hinge variable, antero-posterior respiratory-feeding current, with incurrent and excurrent mantle openings located so as to accommodate such a flow. Ctenidia are reduced, limited to inner demibranchs; individuals are monoecious, with evidence of brooding of young in mantle cavity; frequently commensal or parasitic. These features are characteristic of the bivalves found off northwestern Peru in *Aphrodita,* and they are, therefore, included in the Lasaeidae.

Although adult specimens of the new species assume an exaggerated crescent shape, their shells in many ways resemble those of members of only one generic group so far as I have been able to determine, the genus *Pseudopythina* Fischer, 1878. They share a number of similarities with

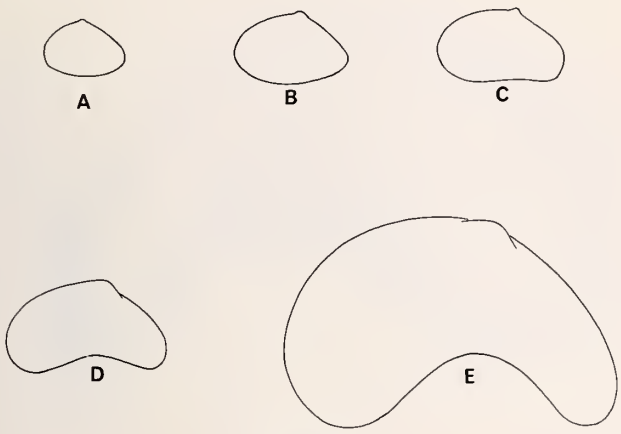

Figure 2

A–E show changes in outline of *Pseudopythina* ***muris*** spec. nov. shells from equilateral to inequilateral as growth progresses.

species assigned to that group, including a tendency to associate with *Aphrodita* and certain crustaceans.

Pseudopythina Fischer, 1878

Pseudopythina Fischer, 1878:178; type species by monotypy, *Kellia macandrewi* Fischer, 1867:194.

Pseudopythinia Locard, 1892:317 [invalid emendation for *Pseudopythina* Fischer, 1878]; Locard, 1898:303.

The type species, *Kellia macandrewi* Fischer, is an inhabitant of southern European seas. Its characteristics were pointed out by Chavan (1969) in his description of *Pseudopythina*: "transverse trigonal, very inequilateral, anteriorly attenuated and elongate; enlarged and rounded backward [posteriorly], smooth." Hinge teeth are simple and consist of a single curved, projecting cardinal tooth in either valve, just beneath the umbos, posterior to which is located a well developed, and mostly internal ligament. The other cardinals and anterior and posterior lateral teeth are much reduced and limited to weak thickenings of the dorsal valve margins. Cardinal teeth of the type species, *P. macandrewi,* are more heavily developed than in other species examined, and may be supported by basal thickening. The anterior adductor muscle scar is usually elongate, the posterior more rounded. A pallial line is evident in some species, usually well inset from shell margins. Externally, shells are smooth with a thin, often wrinkled periostracum, which may be reflected onto the interior edge of the shell. Faint radiating rays are present and are most noticeable at the ventral margin. Shells often show a ventral embayment developed variously in different species; strongest in the new species described herein. *Pseudopythina compressa* Dall, 1899, shows little evidence of such an embayment, prompting Dall (1899) to suggest its normal form results from the lack of a commensal relationship, although Oldroyd (1924) stated that all *Pseudopythina* are commensals.

The anatomy of *Pseudopythina* was described and illustrated by Narchi (1969) in his study of the species *P. rugifera* (Carpenter, 1864) and verified by me through examination of the new species from off Peru. I disagree with the transfer by Abbott (1974) of the West Coast species previously assigned to *Pseudopythina* Fischer to *Orobitella* Dall, 1900. The characteristics of *Pseudopythina macandrewi* are quite different from those of the type species of *Orobitella, O. floridana* Dall, 1899, with its regular and often deeply incised concentric sculpture, large rounded to squarish adductor muscle scars, posteriorly displaced umbos, and pellucid shell, or from the similar appearing *Neaeromya* Gabb, 1873 (type species, *N. quadrata* Gabb, 1873), with which both Abbott (1974) and Bernard (1983) ally *Orobitella.*

There are representatives of *Pseudopythina* in the several marine faunal regions with the exception of the west Atlantic. An abbreviated catalogue of the Recent species follows. Until the anatomy of each species is studied and compared, however, it will not be possible to state with certainty whether or not these species are really related.

East Atlantic

Pseudopythina macandrewi (Fischer, 1867):194 (Nord de l'Espagne; bassin d'Arcachon (Gironde) [Bay of Biscay, France]); not in Journal de Conchyliologie Type Collection (Fischer-Piette, 1950); may be in British Museum (NH) (Dance, 1966); syntypes (?) *ex* MacAndrew in Jeffreys Collection, USNM 170637, from Vigo Bay, Spain.

Remarks—This is the type species of *Pseudopythina* Fischer, 1878. It is listed as a junior synonym of *P. setosa* (Dunker, 1864) by Jeffreys (1881), Locard (1898), Chavan (1969), Nordsieck (1969), and Quiles (1973). The last four authors seem to have ignored the statement by Jeffreys (1882) that Dunker's species is the young of *Coralliophaga lithophagella* (Lamarck, 1819), a member of the Trapeziidae (see Lamy, 1920:283). The name specified by Jeffreys (1882) as having priority over *P. macandrewi, Sportella caillati* Conti, 1864, attributed by the latter to "Deshayes, 1852," apparently is a manuscript name. The name was validly introduced by Deshayes (1860:596) for an unrelated fossil. So far as I can determine, Fischer's name, *Kellia macandrewi,* is the oldest valid taxon for this entity.

Other east Atlantic species assigned to *Pseudopythina* are:

Pseudopythina geoffroyi geoffroyi (Payraudeau, 1826), Nordsieck (1969:90)

Pseudopythina geoffroyi complanata (Philippi, 1836), Nordsieck (1969:90).

Remarks—I have been able to find no information on commensalism in these species.

East Pacific

Of the several east Pacific species included in *Orobitella* Dall, 1900, by Abbott (1974), the only three that seem

to be referable to *Pseudopythina* are listed below. The remainder probably belong in *Orobitella* or other groups. Their ultimate placement will depend on analysis of anatomical relationships impossible at this time.

Pseudopythina rugifera (CARPENTER, 1864):602, 643 (Puget Sound; syntypes USNM 4445); CARPENTER, 1865: 57.

Remarks—Although this species is dated from Carpenter, 1864, without a prior concept it is difficult to recognize without reference to the type specimens. His 1865 description is much more complete. NARCHI (1969), who has made the most intensive studies on this species to date, discussed its anatomy thoroughly and also its commensal relationships with the crustacean *Upogebia* and the polychaete *Aphrodita*. The species is very similar in its general appearance to the new species being described herein, although lacking the extreme crescent shape. The species *P. rugifera* is distributed from Alaska to Baja California, Mexico, according to ABBOTT (1974). The following are synonyms of *P. rugifera* according to BERNARD (1983:32): *Lepton rude* Whiteaves, 1880, *Sportella californica* Dall, 1899, and *Pseudopythina myaciformis* Dall, 1916.

Pseudopythina stearnsii (DALL, 1899):879, 885 (Gulf of California; holotype USNM 73701). BERNARD, 1983:32.

Remarks—*Sportella stearnsii* Dall, 1899, is placed by BERNARD (1983, as *Neaeromya*) close to *P. rugifera* and *P. compressa*. The unique holotype has a much heavier shell and cardinal teeth than the other West Coast species, more reminiscent of the type species, *Pseudopythina macandrewi* (Fischer, 1867).

Pseudopythina compressa DALL, 1899:880, 888 (south of Nunivak Island [SW of Hagemeister Island, USFC sta. 3305], Alaska; holotype USNM 107855).

Remarks—This species is less inflated and has a more rounded outline than *P. rugifera*, but has the characteristic single cardinal tooth and ligament of *Pseudopythina*. DALL (1899) pointed out that, due to its uniform shape, it probably is not a commensal species. Most distributional records for this species are from northern waters, Alaska, north of the Aleutian Islands, south to British Columbia, in from 10 to 150 m (BERNARD, 1983). The record mentioned by ABBOTT (1974), off Acapulco, is based on USNM 210171, USFC station 3422, in 258 m, a typical specimen. The species is listed by HABE (1977) as a *Squillaconcha*, (see below).

Indo-Pacific

Subgenus *Squillaconcha* KURODA & HABE, 1971:627, 404; type species by original designation: *Kellia subsinuata* Lischke, 1871.

Remarks—This taxon was proposed at subgeneric rank to contain Japanese species formerly assigned to *Pseudopythina*. Its justification seems to be based mainly on the geographical and host differences.

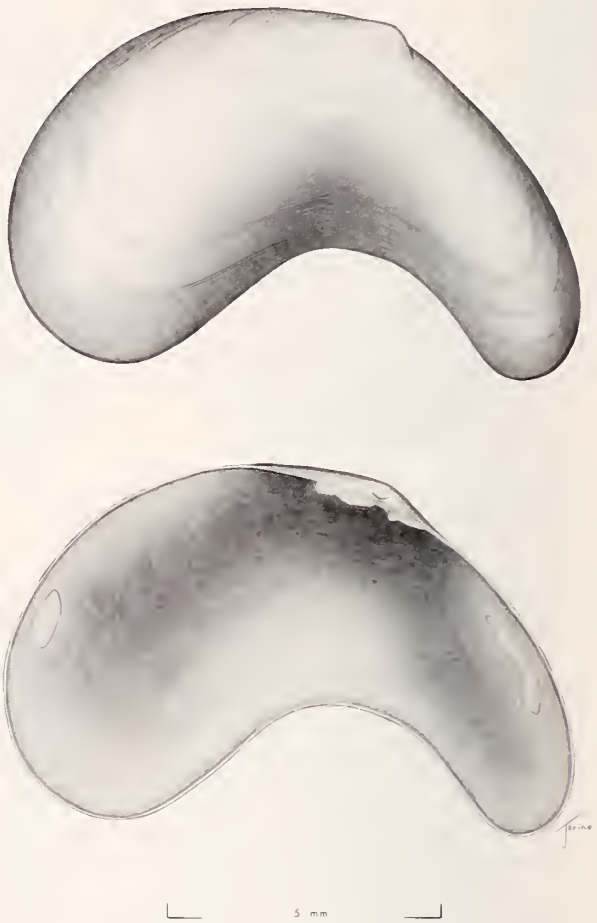

Figure 3

Shell of *Pseudopythina* ***muris*** spec. nov. Upper figure: exterior. Lower figure: interior of shell showing anterior (right) and posterior adductor muscle scars and characteristics of the hinge.

Pseudopythina (*Squillaconcha*) *subsinuata* (LISCHKE, 1871):43 (Japan; type in Academy of Sciences, Leningrad).

Remarks—This species often is found as a commensal on mantis shrimps. It is distributed in Japan on the islands of Honshu, Shikoku, and Kyushu. According to HABE (1964) it incubates its larvae in the branchial chamber.

Pseudopythina (*Squillaconcha*) *sagamiensis* HABE, 1961: 151 (Zushi City, Kanagawa Prefecture, Japan; type in National Science Museum, Tokyo).

Remarks—*Pseudopythina sagamiensis* was added to *Squillaconcha* by HABE (1977), who also included *P. compressa* Dall, 1899, which is here referred to *Pseudopythina* sensu stricto. *Pseudopythina sagamiensis* is said to differ from *P. subsinuata* in being more narrowly elongate and smaller in size than the former. Its commensal relationships apparently are unknown.

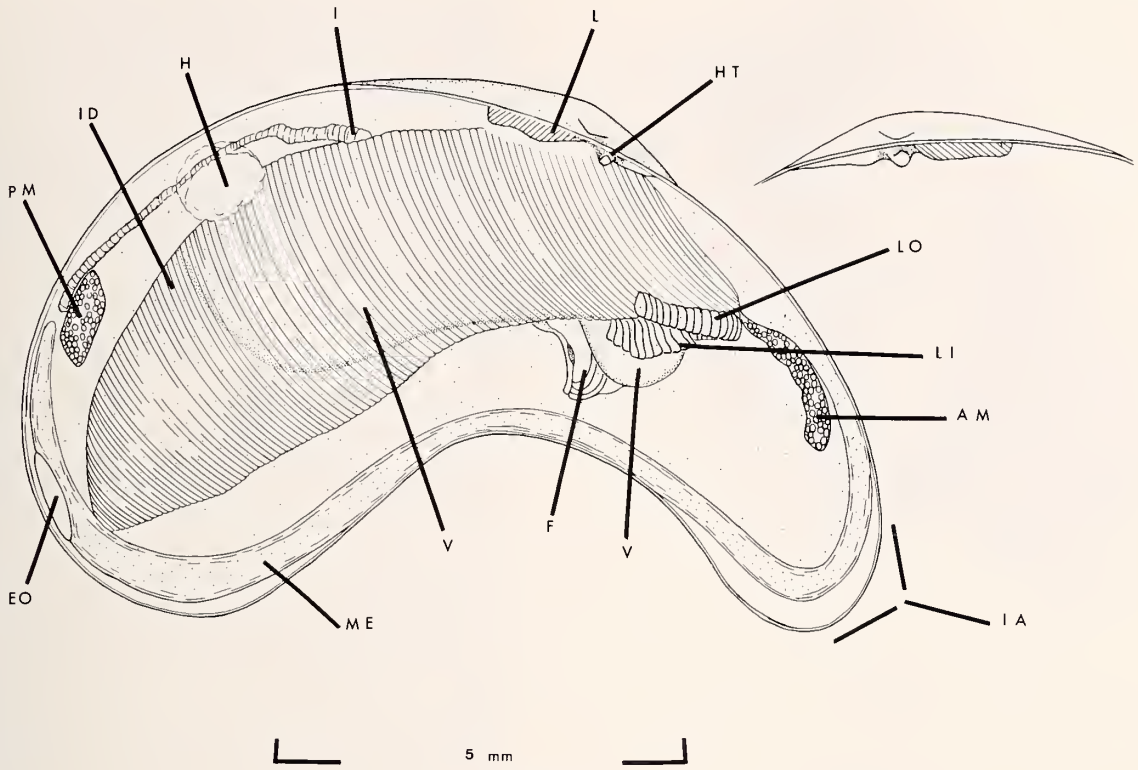

Figure 4

Anatomy of *Pseudopythina* ***muris*** spec. nov. and detail of hinge of right shell valve (see Abbreviations listed at end of text).

Pseudopythina ***muris*** Rosewater, spec. nov.

(Figures 3, 4; Table 1)

Description: Shell reaching 10.9 mm in length; mature individuals have a crescent-shaped outline; valves inflated posteriorly and narrowed anteriorly. Valves thin and translucent, but not excessively fragile; color gray externally where not covered with thin, light-yellow periostracum; internally valves smooth, porcelaneous, and shining. External surface smooth. Radial sculpture of fine threads originating at umbos and radiating anteriorly, posteriorly, and ventrally to shell margins. Threads visible from internal surface by transmitted light. Concentric sculpture consisting of well-marked lines of growth accentuated by areas of crowding which outline transition in shell shape from only moderately to strongly inequilateral. Dorsal margin broadly convex in mature individuals; ventral margin markedly concave. Distance from umbos to posterior margin exceeds distance from umbos to anterior margin. Shell posteriorly hypertrophied, possibly for brooding. Hinge teeth consist of single small, protruding, peg-like cardinal in each valve which interdigitates with its counterpart just anterior to internal opisthodetic ligament that helps join valves. Dorsal margin thickened for considerable distance both anterior and posterior to umbos. Umbos directed antero-medially. Pallial line not evident. Anterior adductor muscle scar hardly visible, long and narrow as interpreted from animal's anterior muscle; posterior adductor muscle scar less elongate than anterior scar. Prodissoconch small (about 30 μm in length) fan-shaped, shining.

Animal with thickened mantle edge; mantle open antero-ventrally forming incurrent-pedal aperture area. Well-marked excurrent aperture located posteriorly. Mantle open from ventral border of excurrent aperture to region of lower border of anterior adductor muscle scar. Ctenidium consists of only single demibranch, probably the inner, but there appear to be both inner and outer labial palps. Foot small, with well-marked byssal groove.

Holotype: USNM 836636; from R/V *Anton Bruun* SEPBOP Cruise 18B, Station 764; Lat. 4°06'S; Long. 81° 09'W; off NW Peru; 90 m; 8 September 1966; length 10.7 mm; height 6.6 mm.

Paratypes: 51 paratypes USNM 836637; from same station; ranging in length from 1 to 10.9 mm; height from 0.8 to 7.4 mm.

Other specimens: 4 specimens USNM 836638; from R/

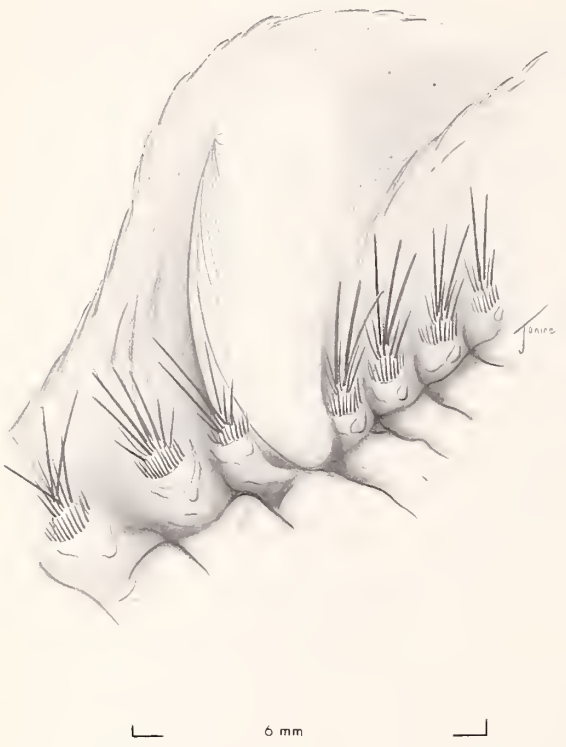

Figure 5

Detail showing anterior end of a *Pseudopythina* ***muris*** spec. nov. protruding from between parapodia of *Aphrodita japonica.*

V *Anton Bruun* SEPBOP Cruise 16, Station 625a; Lat. 4°57′S to 5°01′S; Long. 81°23′W; off NW Peru; 118–133 m; 2 June 1966; ranging in length from 2.6 to 5.1 mm; height from 1.8 to 2.7 mm.

Etymology: *muris*—genitive singular of the feminine (or masculine) Latin substantive noun *mus* (mouse), meaning "of the mouse," alluding to the presence of *Pseudopythina* ***muris*** spec. nov. in the respiratory cavity of the seamouse *Aphrodita japonica* Marenzeller, 1879.

Remarks: *Pseudopythina* ***muris*** spec. nov. was found in the respiratory cavity of *Aphrodita japonica* at two R/V *Anton Bruun* stations in 90–133 m, from off northwestern Peru in June and September 1966. The fact that at least 52 bivalves were found in 7 worms from one of the stations indicates that this probably is not an adventitious relationship, although the other bivalve living with *Aphrodita* in the east Pacific, *Pseudopythina rugifera,* also inhabits a crustacean. In some cases, commensal relationships may be purely fortuitous and based on the availability of a suitable substratum, which happens to be another animal. In this case the clam appears to be at least partially adapted to the *Aphrodita* host. The first individuals noticed were attached by byssal threads to the ventral surfaces of the *Aphrodita* in the vicinity of the parapodia. Those discovered within the respiratory chamber of the worms were byssally attached to the surfaces of the worms' elytra, and on at least two occasions, mature *Pseudopythina* ***muris*** were found with their anterior ends protruding from between two parapodia outside a worm's respiratory chamber

Table 1

Measurements of *Pseudopythina* ***muris*** spec. nov. from R/V *Anton Bruun* SEPBOP Cruises 16, Station 625a, and 18B, Station 764 (N = number of individuals in sample; M = arithmetic mean; SD = standard deviation; V = variance; H/L = ratio of shell height to length produced by dividing height by length).

	Station 764							Summary	
	Clams in worm 1	Clams in worm 2	Clams in worm 3	Clams in worm 4	Clams in worm 5	Clams in worm 6	Clams in worm 7	Station 764	Station 625a
N	21	6	6	5	5	5	4	52	4
Length (mm)									
Range	1.0–10.7	1.8–9.6	1.4–10.7	1.4–10.9	1.6–10.7	2.1–3.2	1.8–4.8	1.0–10.9	2.6–5.1
M	2.20	3.40	3.13	5.36	3.88	2.44	3.45	3.03	3.75
SD	1.94	2.80	3.39	4.25	3.44	0.42	1.25	2.77	0.89
V	3.75	7.84	11.48	18.08	11.81	0.18	1.55	7.69	0.79
Height (mm)									
Range	0.8–6.4	1.3–6.4	1.0–6.9	1.1–7.4	1.0–6.6	1.4–2.1	1.3–2.4	0.8–7.4	1.8–2.7
M	1.50	2.20	2.13	3.64	2.36	1.58	1.93	1.99	2.18
SD	1.12	1.87	2.14	2.87	2.14	0.27	0.42	1.76	0.33
V	1.25	3.48	4.56	8.25	4.57	0.74	0.18	3.08	0.11
H/L									
Range	0.60–0.80	0.62–0.72	0.65–0.79	0.64–0.79	0.39–0.72	0.62–0.67	0.49–0.72	0.39–0.80	0.53–0.69
M	0.71	0.67	0.72	0.69	0.62	0.65	0.60	0.68	0.59
SD	0.05	0.03	0.04	0.05	0.12	0.02	0.10	0.07	0.06
V	0.002	0.001	0.002	0.003	0.141	0.0004	0.010	0.005	0.107

(Figure 5). It is assumed this situation would provide the clam with a direct source of fresh seawater for feeding and respiration while the clam's posterior portion is well protected inside the worm's respiratory cavity.

Although the clams have not been sectioned to determine their sexuality, leptonaceans are known to be monoecious, and this mode of reproduction certainly would be advantageous to an animal that may be isolated in a worm's respiratory cavity. How clams travel between hosts is unknown. Leptonaceans are known to walk, however, and young may be drawn into a worm's respiratory cavity through its incurrent points. Frequently there is a range of individuals present in a worm, from smallest to largest sizes (Table 1). Usually there is only a single large individual, but, in two cases, two large individuals were present in a worm. The other clams present are mostly of smaller sizes: 1–5.1 mm in length. It is strongly suspected that these young are produced ovoviviparously via a brood pouch occupying the hypertrophied, globose posterior ends of the larger specimens (see Figure 1, showing X-rays taken from different angles to reveal expanded nature of shells). An example of the pattern of distribution of different sized clams in a worm is shown in the drawing (Figure 6).

In the adult stage, *Pseudopythina* ***muris*** is easily distinguished from the other West Coast *Pseudopythina* due to its exaggerated crescent shape and hypertrophied posterior. The other species are oval to subrhomboidal in outline, although there is clear evidence of an embayment in the ventral margin of *P. rugifera* (see discussion under *Pseudopythina*). *Pythinella sublaevis* (CARPENTER, 1857: 112) frequently has shell curvature, but it differs from *Pseudopythina* in hinge morphology and is unrelated.

The unusual shape of *Pseudopythina* ***muris*** may be an adaptation to life in the respiratory cavity of *Aphrodita.* The oddly shaped shells of other Leptonacea provide evidence of functional adaptations. *Curvemysella paula* lives in association with a hermit crab (HABE, 1959). Similarly, bivalves such as *Rochefortia* and *Pythinella,* with curved ventral margins, nestle in apertures and boreholes of gastropod shells where the curvature provides a secure purchase (personal observations). The shell of *Aligena cokeri* Dall, 1909, is grooved from near the umbos to its ventral margin, reflecting a mid-ventral byssal attachment to the tube of the Panamic polychaete *Mesochaetopterus alipes* Monro, 1928 (also see MONRO, 1933, and ROSEWATER, 1976). When the mode of life of these and other aberrant-looking bivalves is understood, there is often a functional explanation for their peculiar appearances.

Further testimony to the major change in shape undergone during the maturation of *Pseudopythina* ***muris*** may be noted in the table of measurements. There is an especially wide range in the ratio of height to length: 0.39–0.80. This indicates the transition from rather elongate young (0.39) to the mature individuals whose strong crescent shape causes the more nearly 1:1 ratio of height to length.

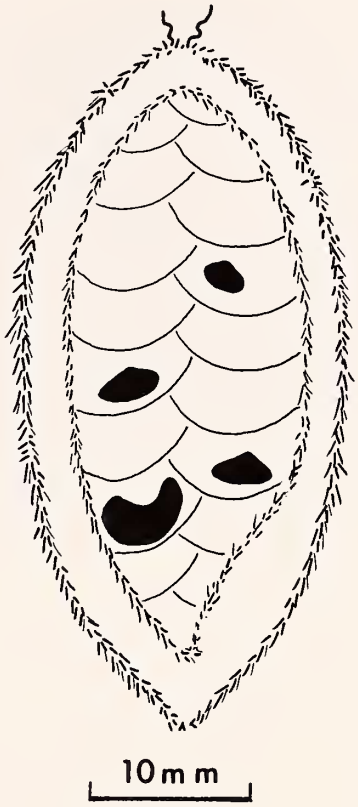

Figure 6

Various growth stages of *Pseudopythina* ***muris*** spec. nov. *in situ,* attached to elytra of *Aphrodita japonica* (dorsal covering of respiratory cavity, or "burlap," is cut away).

ABBREVIATIONS

The following institutional, program, and anatomical abbreviations are used in this paper.

AM	anterior adductor muscle
ANSP	Academy of Natural Sciences of Philadelphia
CAS	California Academy of Sciences
eo	excurrent opening
f	foot
h	heart
ht	hinge tooth
i	intestine
ia	incurrent area
id	inner demibranch
l	ligament
li	inner labial palp
lo	outer labial palp
MCZ	Museum of Comparative Zoology, Harvard University
me	mantle edge
NMNH	National Museum of Natural History, Smithsonian Institution
pm	posterior adductor muscle

SEPBOP South Eastern Pacific Biological Oceanographic Program
USNM United States National Museum (NMNH)
v visceral mass

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Two anonymous reviewers made helpful recommendations among which was the suggestion that I use the superfamily name Galeommatacea in place of Leptonacea, based on date priority. The latter is not a current requirement of the ICZN for names above family level, nor do I consider it a productive procedure in groups such as Leptonacea that are in a state of flux as concerns our understanding of biological and nomenclatorial entities. For those who wish to follow strict date priority to class level in the Bivalvia, BERNARD (1983) includes a great deal of useful and detailed information.

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